# Flash suppression and flash facilitation in binocular rivalry

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We show that previewing one half image of a binocular rivalry pair can cause it to gain initial dominance when the other half is added, a novel phenomenon we term *flash facilitation*. This is the converse of a known effect called *flash suppression,* where the previewed image becomes suppressed upon rivalrous presentation. The exact effect of previewing an image depends on both the duration and the contrast of the prior stimulus. Brief, low-contrast prior stimuli facilitate, whereas long, high-contrast ones suppress. These effects have both an eye-based component and a pattern-based component. Our results suggest that, instead of reflecting two unrelated mechanisms, both facilitation and suppression are manifestations of a single process that occurs progressively during presentation of the prior stimulus. The distinction between the two phenomena would then lie in the extent to which the process has developed during prior stimulation. This view is consistent with a neural model previously proposed to account for perceptual stabilization of ambiguous stimuli, suggesting a relation between perceptual stabilization and the present phenomena.

Keywords: binocular rivalry, flash suppression, ambiguous stimuli, priming, perceptual stabilization

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## Introduction

Ambiguous images are ones that have multiple, mutually exclusive interpretations. Notable examples are the Necker cube and Rubin's face–vase illusion. Binocular rivalry is a form of ambiguous perception that arises when we present two incompatible images to the two eyes, resulting in a percept that wavers between both images, involving the complete perceptual disappearance of the temporarily suppressed pattern. Binocular rivalry can be used as a tool for bringing to light subtle shifts in neural activity that accompany various experimental manipulations. For instance, changes in predominance of one percept over the other have been used to disclose effects of center–surround interactions on visual processing (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006) and to demonstrate the action of so-called Gestalt grouping cues (Alais & Blake, 1999). A particularly sensitive use of rivalry as an indicator of neural state is to simultaneously switch on both competing images and observe which one gains dominance first: Here both neural representations start racing for dominance simultaneously, and even a slight imbalance in the two images' processing may considerably bias initial dominance. For instance, drawing attention to one of two, otherwise balanced, images can cause a threefold to fourfold shift in their initial dominance ratio (Chong & Blake, 2006; Kamphuisen, van Wezel, & van Ee, 2007; Mitchell, Stoner, & Reynolds, 2004). Another well-known example is *flash suppression* (Kreiman, 2001; Wolfe, 1984): Briefly showing one of the competing patterns in isolation can virtually eliminate the possibility of it winning the race upon subsequent rivalrous presentation. Flash suppression is a valuable experimental tool that allows investigators of visual perception and awareness to dictate their subjects' perception of an ambiguous stimulus (e.g., Kreiman, Fried, & Koch, 2002; Sengpiel, Blakemore, & Harrad, 1995; Sheinberg & Logothetis, 1997).

Here we use initial dominance in binocular rivalry to systematically study how prior exposure to a pattern affects

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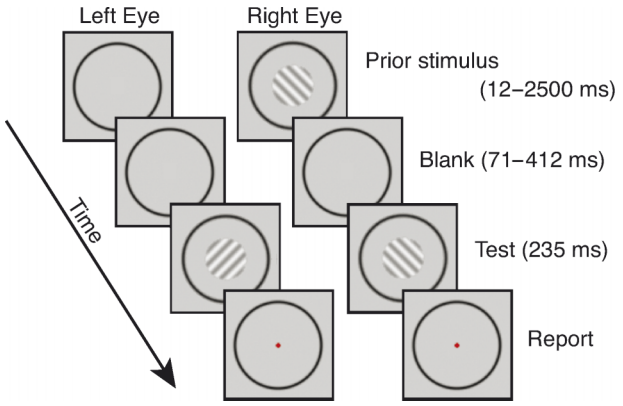


Figure 1. Time course of a trial in the main condition. Subjects consecutively viewed one half of a dichoptic orthogonal grating stimulus (prior stimulus), a blank interval, and both stimulus halves together (test). They then reported which of the two rivaling orientations was perceptually dominant during the test, revealing effects of the prior stimulus. We systematically varied the durations of the prior stimulus and the blank, as shown, as well as the contrast of the prior stimulus. In additional conditions, we varied the nature of the prior stimulus to specifically address eye-based and pattern-based effects and to investigate the importance of the spatial correspondence between prior stimulus and test stimulus. We also varied the luminance of the background to investigate if the relative luminance of the stimulus with respect to its surround affects the observed effects.

subsequent visual processing. We do this (Figure 1) by briefly presenting an image (prior stimulus) and then after a blank interval letting that image compete for dominance against one in the other eye (test). Surprisingly, prior exposure to one of the rival patterns in isolation cannot only impair that pattern's initial dominance (flash suppression) but can also facilitate it, a novel phenomenon that we call *flash facilitation*. The exact effect of a prior stimulus depends on both its duration and its contrast. These two are largely interchangeable, so that (after correcting for a contrast transfer nonlinearity) the effect of a prior stimulus shows a systematic relation with their arithmetic product, here denoted as the "energy" of the prior stimulus. Initial dominance is suppressed by high-energy prior stimuli but facilitated by low-energy ones.

In additional conditions, we vary parameters such as the eye of origin of the prior stimulus relative to the test stimulus. These manipulations indicate that both the facilitatory effect and the suppressive effect at least partly originate in lower visual areas, and that both are built up of an eye-based component and a pattern-based component. In the standard condition, these components add up to jointly produce a prior stimulus' effect.

We discuss our findings in relation to a growing body of literature demonstrating a dual effect of prior exposure in a variety of cognitive and perceptual tasks, as well as possibly related instances of facilitation in nonrivalrous vision. We argue that the most parsimonious interpretation of our findings is not one in which facilitation and suppression reflect entirely distinct mechanisms. Instead, our results are consistent with the idea of a continuous neural process that underlies both facilitation and suppression.

## Methods

Each trial (Figure 1) consisted of the sequential presentation of a prior stimulus, a blank interval, a test, and a fixation dot prompting subjects to report. In most conditions, the test was a pair of dichoptic orthogonal sine wave gratings, oriented ±45° from vertical. In one condition (see below), we used square wave gratings. Subjects fixated the stimuli through a stereoscope at a viewing distance of 47 cm, within a black alignment ring ($r$ = 1.1°, or $r$ = 2.3° for the larger stimuli) on a gray background (30 cd/m$^2$; the stimuli's mean luminance) unless otherwise stated.

Seven subjects participated in the sessions of Figures 2 and 3, four took part in those of Figures 4 and 5. Two authors were subjects in all of these experiments, the others were naive.

Subjects reported which of the two test gratings was perceived more strongly. This instruction allowed them to make a choice even if dominance was incomplete. Subjects could discard a trial if they felt they were unable to make a choice, which happened on 2% of the trials. To verify that our subjects experienced strong rivalry suppression in our experiments, we performed a control experiment (not shown) where normal trials were randomly interleaved with ones where the orthogonal test gratings were presented superimposed to one eye. In those conditions, subjects generally perceived a fairly balanced plaid and they discarded 76% of the trials. This confirms that there was clear rivalry suppression during the test in our experiments.

In the main condition (Figure 1), we used one half of the pair of test gratings as a prior stimulus to differentially address one of the two competing neural representations. Then, there were three conditions that were designed to tease apart the effects of prior stimulation of one eye and prior exposure to a particular pattern, respectively.

1. In the *eye* condition, the prior stimulus was a monocular pattern that was unlike either test grating, namely, concentric rings. Because this prior stimulus did not specifically coincide with either test pattern, it allowed us to single out eye-of-origin effects.
2. The *pattern* condition had the complementary objective of isolating pattern related effects on initial dominance. Here, like in the main condition, the prior stimulus consisted of one of the two test patterns, but we presented it to both eyes. Because this prior stimulus did not specifically target either eye, it formed a probe into pattern related effects.

3. In the *swap* condition, the prior stimulus consisted of one eye's test pattern, but presented to the opposite eye (i.e., the pattern was swapped between eyes in between prior stimulus and test). This condition bypassed any effects of the prior stimulus on monocular orientation channels and allowed us to further constrain the source of the observed effects.

Two further conditions were designed to assess the importance of the spatial correspondence between the prior stimulus and the test stimulus.

1. The *annulus* condition was similar to the main condition, but here the prior stimulus was an annulus that surrounded the location of the test stimulus. Any retinotopic effects should disappear here.
2. The *phase shift* condition was similar to the *pattern* condition, but it involved a phase difference between the prior stimulus and the test stimulus, allowing further inferences on the neural location of the effects.

In a final condition, we investigated if the results from a classic flash suppression study (Wolfe, 1984) would be affected by changing the luminance of the stimulus' background. For that condition, we used a square wave grating similar to the one used in the original study.

For all conditions, the test duration was 235 ms, a duration sufficiently long to allow rivalry to develop (e.g., Chong & Blake, 2006; Wolfe, 1983; Wolfe, 1984) but too short for perceptual alternations to occur. Test contrast was 50% Michelson unless otherwise stated. For the main condition, we parametrically varied the contrast and duration of the prior stimulus from 2.7% to 100% Michelson and from 12 to 2500 ms, respectively, and the duration of the blank from 71 to 412 ms. In the other conditions, we applied only a subset of durations and contrasts and used only a 71-ms blank unless otherwise stated. The sine wave gratings (3.6 c/deg) filled a circular patch of radius 0.55°, except in the phase shift condition, where we used a larger stimulus ($r$ = 1.4°; 1.4 c/deg) to minimize the effect of eye movements. The concentric rings used for the eye condition (5.2 c/deg) were designed to equate the gratings in total contour length. The ring pattern's contrast fell off along a Gaussian profile ($\sigma$ = 0.14°) at the edge so that even the outlines did not coincide between prior stimulus and test. In the annulus condition, the annulus had an inner and outer radius of 0.61° and 1.1°, respectively. In the experiment replicating Wolfe's data and investigating the role of background luminance, we copied Wolfe's original stimulus with some slight modifications. That is, we used diagonal square wave gratings ($r$ = 1.35°; 3.8 c/deg) and 90% Michelson contrast for the test stimulus.

We randomly interleaved the main condition, eye condition, pattern condition, and swap condition within sessions. We also randomized the relation between orientation and eye during the test, as well as the eye receiving the prior stimulus. Randomization of conditions minimizes the interaction between consecutive trials, such as observed in "perceptual stabilization" (Leopold, Wilke, Maier, & Logothetis, 2002). Randomization of the eye and the orientation has the same effect, as well as allowing us to control for systematic biases toward one orientation or eye. All data figures show pooled data over all eye–orientation combinations, with about 50 observations underlying each data point for each subject.

# Results

## Flash suppression and flash facilitation

Figure 2 shows the subject-averaged results from our main condition, in which the prior stimulus was one half of a pair of dichoptic orthogonal gratings (top right inset). The key finding here is that prior exposure can both suppress and facilitate dominance of the previewed pattern. The top panel shows results using a 71-ms blank between prior stimulus and test. Facilitation occurs when the prior stimulus is weak, being either of short duration (leftmost sections of the curves) or of low contrast (lighter shaded curves). Suppression, on the other hand, follows long, high-contrast prior stimuli. Contrast and duration are to some extent interchangeable, as the curve shifts rightward with decreasing contrast. All facilitatory effects dissipate within hundreds of milliseconds after the offset of the prior stimulus, as seen in the bottom panels, which show the outcome at larger blank durations. Note that these plots, as well as the remaining ones, represent pooled data from trials where the prior stimulus could be presented to either eye and could have either orientation, and the two test patterns were distributed to the eyes accordingly. Any systematic bias in rivalry dominance toward one eye or orientation will therefore cancel out in these representations, and one may safely interpret any deviations from 0.5 as effects of the prior stimulus.

## Eye effects versus pattern effects

Because in the main condition we used one of the two test patterns as a prior stimulus, our results could in principle be the result of prior stimulation of one eye, prior exposure to one pattern, or both. Figure 3 shows the outcome of experiments that dissociate these options. Here we define "pattern facilitation" and "pattern suppression" as the tendency for the previewed pattern to become dominant or suppressed during the test, respectively. The terms "eye facilitation" and "eye suppression" refer to dominance or suppression, respectively, of the eye that received the prior stimulus. Isolating eye effects (panel a) by stimulating one eye with a pattern unlike either test pattern (concentric

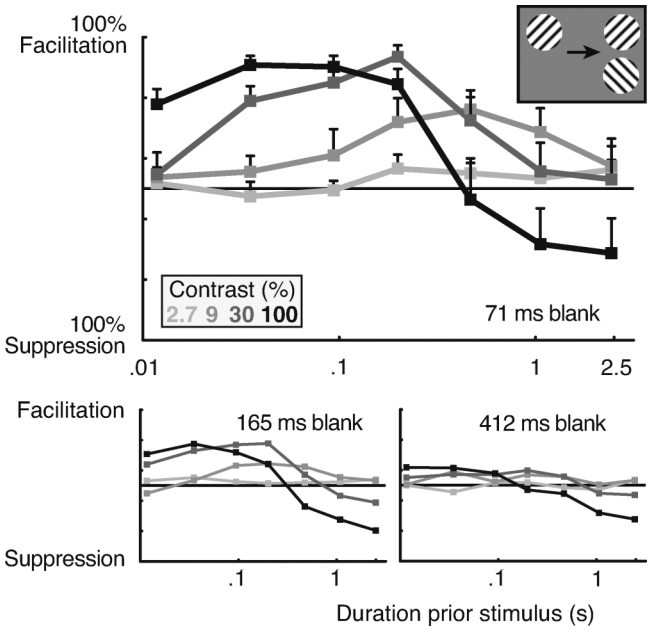


Figure 2. Dominance as a function of the duration and contrast of the prior stimulus in the main condition. The top panel shows the results for the shortest blank duration (71 ms). Considering first the black curve (100% prior stimulus contrast), we see a biphasic effect of the duration of the prior stimulus: Brief exposure to one stimulus half enhances its subsequent dominance (facilitation), but exposure durations over about.5 s have the opposite effect (suppression). The other curves in this panel indicate that decreasing the contrast of the prior stimulus causes this evolution to slow down, as well as reducing its amplitude. These differences are significant: Taking, for all subjects separately, the location and the height of each curve's highest point, contrast correlates negatively with log peak time ($p < .05$) and positively with peak amplitude ($p < .05$). The two bottom panels show a rapid decay of facilitation at increasing blank durations, and much less so of suppression. Error bars (not shown in the bottom panels) are standard errors of the mean ($n = 7$; see Appendix A for individual subjects' data).

rings) yields results similar to those in the main condition: Eye dominance is facilitated by brief or low-contrast prior stimuli and suppressed when using a longer duration or a higher contrast. We take this to be a general eye effect, not an orientation-specific effect that is due to the minor orientation correspondence that exists between the rings and the gratings. This interpretation is strengthened by the fact that we get similar results when using a vertical grating or a luminance patch as a prior stimulus (data not shown).

Surprisingly, the complementary condition (panel b), wherein we single out pattern-specific channels by presenting one of the two test patterns to both eyes during prior stimulation, again produces comparable results. Thus, eye-based effects and pattern-based effects show a similar dependence on the parameters of the prior stimulus and jointly underlie the outcome of our main condition.

The effects shown in Figure 3a (eye condition) necessarily originate at processing levels where both monocular streams have not yet fully converged. What channels underlie the data in panel b (pattern condition), however, is less clear-cut. It seems clear that pattern selective channels are involved, but are these monocular or binocular? Panel c addresses this question, showing what happens when we let one eye preview the other eye's test grating (swap condition). This bypasses effects in monocular orientation detectors, so if these are responsible for the outcome of the pattern condition, we expect only a general eye-based effect here and predict results similar to those of panel a (eye condition). If, on the contrary, the outcome of the pattern condition has a binocular origin, it is pitted against eye-based effects here, presumably yielding an outcome that is a trade-off between both forces. Panel c strongly points to the latter option, showing a result that is clearly different from that of the eye condition in panel a, and that could well be due to the opposed action of eye-based effects and pattern-based effects. In fact, the curves in panel c are similar to the arithmetic difference between those found for the eye condition (panel a) and those found for the pattern condition (panel b). This is quantified in panel d. The *Y*-axis here depicts the outcome of the swap condition, for each combination of subject, contrast and duration separately. The *X*-axis depicts a prediction for the corresponding combinations, calculated by subtracting the outcome of the pattern condition from that of the eye condition (as indicated by the icons on the axis). Although this linear subtraction is arbitrary, the positive trend is clearly consistent with a trade-off between both forces. These findings therefore indicate that the pattern-based effects at least partly arise at stages beyond binocular convergence and exist independent of the eye-based effects.

Incidentally, the findings in Figure 3 also rule out the option that facilitation is due to a cognitive bias to report the previewed pattern. First, neither of the rival patterns was previewed in the eye condition (Figure 3a). Second, the conditions of Figures 2 and 3 were interleaved randomly and could not be distinguished by the subjects, yet the tendency to report the previewed pattern is absent in the condition of Figure 3c (for further evidence against this concern, see Appendix A).

## Retinal location and phase

To further elucidate the neural basis of the observed phenomena, we tested their dependence on the spatial correspondence between the prior stimulus and the test stimulus: their relative retinal location and relative phase. Figure 4a shows data from a condition where the location of the prior stimulus did not coincide with that of the test patch but instead surrounded it. In this condition, the facilitatory effect is largely abolished, indicating a high degree of retinal specificity. Regarding suppression the data are less conclusive as suppression was weak even in the baseline condition. Figure 4b shows that phase

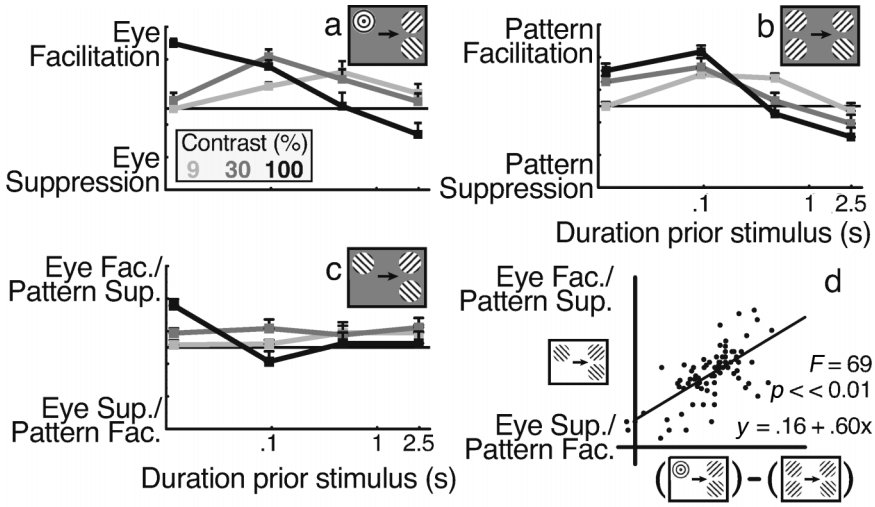


Figure 3. Dissociating eye-based effects and pattern-based effects. (a) Eye condition: Prior stimulation of one eye using a pattern that is unrelated to either test pattern causes facilitation and suppression much like in the main condition. The converse condition of previewing one test pattern dioptically (b, pattern condition) again has a comparable effect. Clearly, eye-based effects and pattern-based effects obey similar laws, and both contribute to the outcome of our main condition. If as a prior stimulus we let one eye view the opposite eye's test pattern (c, swap condition), the pattern-based effects and eye-based effects largely cancel out. In panel d, the *Y*-axis depicts the outcome of the swap condition for each combination of subject, contrast, and duration. The *X*-axis depicts the difference between the outcome of the eye condition and the pattern condition for the corresponding combinations. This difference turns out to form a fair prediction for the outcome of the swap condition. This underscores that eye-based effects and pattern-based effects act against each other in the swap condition. Panels a–c show subject-averaged data; error bars are standard errors of the mean ($n = 7$). Like in the main condition, contrast correlates negatively with log peak time ($p < .05$) and positively with peak amplitude ($p < .05$) for the curves of the eye and pattern condition. For the swap condition, the correlation with peak amplitude remains, but the one with log peak time is no longer significant.

differences have no influence in case the prior stimulus has a low contrast, but that at a high contrast they do cause a shift toward suppression. This combination of retinal specificity, partial (but not complete) phase dependence, and both monocular and binocular components (Figure 3) suggests a distributed neural origin with an emphasis on lower visual areas.

## Comparison with flash suppression studies

We wondered how the current experiments could give rise to such pronounced facilitatory effects, considering that previous studies found only suppressive effects of showing one of the rival patterns as a prior stimulus. Although this can partly be attributed to the long, high contrast prior stimuli that are often used, we explored two additional options.

First we examined whether the fact that many studies excluded a blank interval between the prior stimulus and the test could be a relevant factor. Figure 5a shows results from an experiment where we systematically varied the blank duration, using the same stimulus as in our main condition. The plot shows that without a blank interval (blank duration 0 s), suppression is somewhat stronger than at the blank duration we used (71 ms; dashed vertical line). More specifically, it appears that at blank durations above about 50 ms there is a continuous evolution of the effect of the prior stimulus. In some cases (12.5% and 25% contrast), this is simply a gradual decline, and in others (50% and 100%) this involves an excursion toward suppression before the effect is extinguished. At shorter blank durations (0 and 12 ms, leftmost points), the curves appear to depart from this gradual progression and show a shift toward suppression (this discontinuity is marked by dashing of the curves).

A second factor we examined is the luminance of the background on which the stimuli are presented. It is common to use a black background in experiments such as these, whereas in the present experiments the background was grey, equal to the mean luminance of the stimuli. To make a more direct comparison with existing flash suppression studies, we copied the stimulus from a classic study that used a black background (Wolfe, 1984). This is a square wave grating somewhat larger than our basic stimulus. In one condition, we attempted to replicate that study's results by using the original black background; and in a second condition, we raised the background luminance to equal the mean luminance of the stimulus. Figure 5b depicts the outcome of these experiments. Using a black background (top), we found robust suppression, in agreement with the original study (the star indicates the settings of that study's main experiment). With this background luminance, facilitation remained weak or absent even at a lower contrast

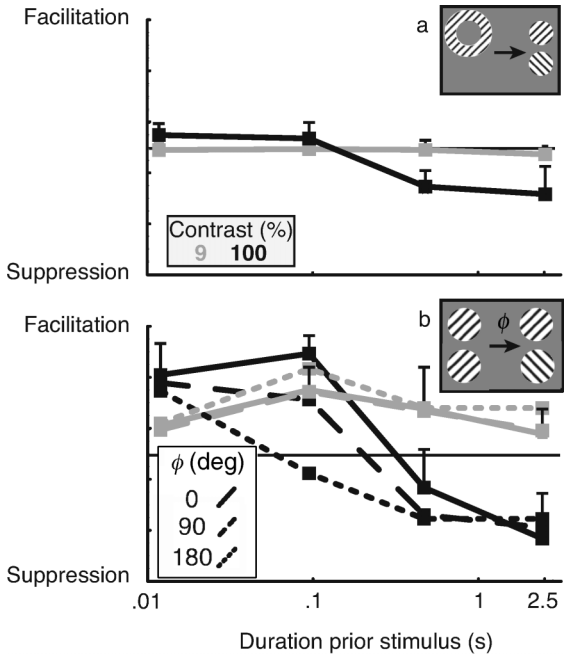


Figure 4. The influence of the spatial relation between the prior stimulus and the test stimulus. (a) When the retinal location of the prior stimulus does not coincide with that of the test stimulus, its effect is negligible (none of the points here differs significantly from chance; two-sided *t* test; $p > .05$). (b) A phase difference ($\varphi$) between the prior stimulus and the test stimulus preserves the basic effect, but with an increased tendency toward suppression when using a high-contrast prior stimulus. This difference is significant for the 90-ms prime, when comparing $\varphi = 0°$ with $\varphi = 180°$ (two-sided paired *t* test; $p < .01$). These features, together with those shown in Figure 3, are consistent with a distributed neural basis that includes lower visual areas. Error bars, only shown for $\varphi = 0°$ in panel B, are standard errors of the mean ($n = 4$).

and duration of the prior stimulus. However, when the background luminance was increased (bottom), we again observed the familiar pattern of strong facilitation and slight suppression seen in our main experiments. Clearly, background luminance is another important factor affecting the balance between flash facilitation and flash suppression. Note that in Wolfe's original experiments, suppression may have been even stronger due to a much higher luminance difference between background and stimulus. We could not apply this difference because the mean stimulus luminance on Wolfe's tachistoscope (398 cd/m$^2$) is well beyond our CRT monitor's capacity (our mean luminance was 30 cd/m$^2$).

## Energy of the prior stimulus determines facilitation and suppression

We have shown that the contrast and the duration of the prior stimulus are to some extent interchangeable: Lower contrast prior stimuli need to be presented longer to reach their maximal effect. Therefore, we may be able to unify the outcomes from all contrasts by using some measure of stimulus energy, that is, "power" × duration. This is shown in Figure 6a. Here we replot the data from Figure 2, as a function of the prior stimulus' contrast$^{0.75}$ × duration. Plotted in this way, the course of the curves practically coincides for all contrasts (For instance, compare the

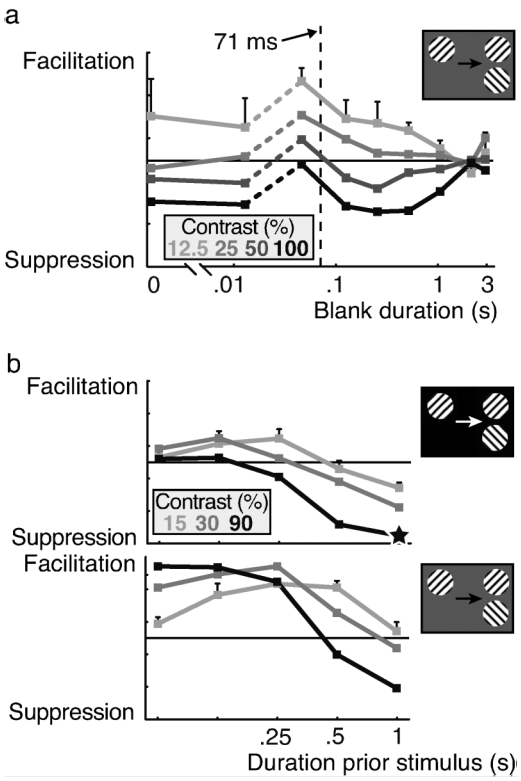


Figure 5. Factors that shift the balance between facilitation and suppression. (a) Removing the blank interval. At blank durations above about 50 ms (we mainly used 71 ms, dashed vertical line), there appears to be a continuous evolution of the effect of the prior stimulus. Shorter blanks, however (0 and 12 ms, leftmost points), yield an increased suppression that seems discontinuous with the remainder of the curves (marked by dashing). This shows that leaving out the blank interval weakens facilitation. The duration of the prior stimulus was 800 ms here. (b) Background luminance. Top: Using a stimulus from a classic flash suppression study (Wolfe, 1984), we found mainly suppression, even if the contrast and the duration of the prior stimulus were relatively low. After raising the background luminance from black to the stimulus' mean luminance, however, the same stimulus produced mainly facilitation. Background luminance, therefore, is a key parameter. Suppression is significantly stronger in the black background condition for all points in these plots, apart from the two briefest prior stimuli at minimal contrast and the longest one at maximal contrast (one-sided paired *t* test on individual subjects' data; $p < .05$). Error bars (only shown for lowest contrasts) are standard errors of the mean ($n = 4$).

locations of the maxima). A parsimonious explanation of this invariant "energy" is that facilitation and suppression depend on a continuous neural process that occurs progressively during the presentation of the prior stimulus, and at a rate proportional to the contrast of that stimulus.

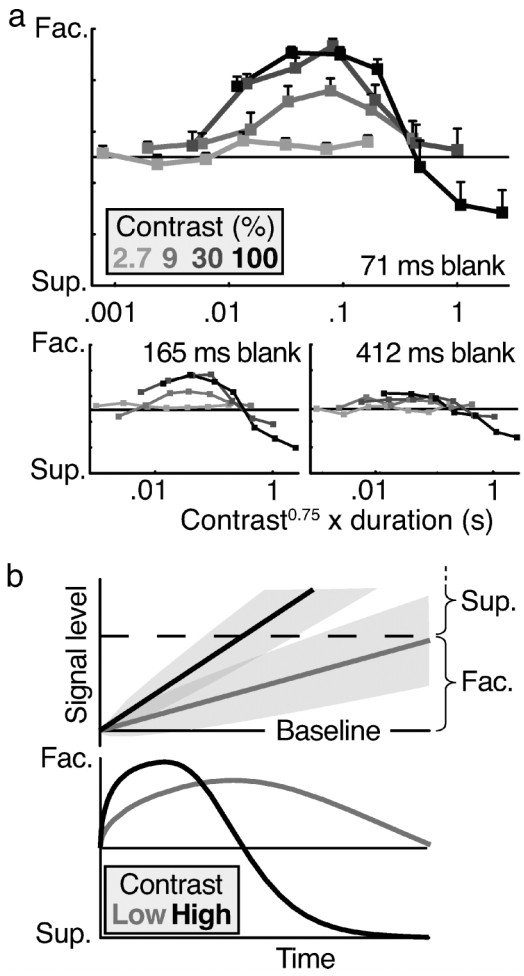


Figure 6. A single progressive process may underlie both facilitation and suppression. (a) The data from Figure 2 replotted as a function of the "energy" of the prior stimulus: Contrast$^{0.75}$ × duration. In this representation, the course of all curves corresponds closely (the exponent of 0.75 was chosen by eye). This suggests a mechanism such as schematically illustrated in panel b. A signal builds up linearly during the presentation of the prior stimulus (top panel), at a rate proportional to contrast$^{0.75}$. If by the end of the prior stimulus' presentation the signal lies between baseline and a certain threshold (dashed line), this yields facilitation, whereas if it rises beyond this threshold or ends up below baseline, we get suppression. Such a scenario would also explain the different curve amplitudes as due to different noise levels in the accumulated signal (shaded areas): A signal that is twice as weak needs twice as much time to reach the same end level, but, assuming it is integrated with additive noise, four times as much to reach the same signal-to-noise ratio. The bottom panel shows facilitation and suppression corresponding to the top panel signals.

This is illustrated schematically in Figure 6b. Here a hypothetical "signal" rises linearly during the presentation of the prior stimulus (Figure 6b, top panel), with a rate of rise that is a function of its contrast (light versus dark curve). If we further assume that a low end-level of this signal produces facilitation, whereas a high end-level yields suppression, we obtain an outcome (bottom panel) very similar to our experimental results (see Discussion for a further remark on this assumption). The deviations between the curves' amplitudes, evident both in our empirical data (Figures 2, 3, 4, 5, and 6) and the bottom panel of Figure 6b, are now a natural consequence of adding noise to the accumulating signal. That is, a lower rate of rise causes a greater spread in the total accumulated value, as indicated by the shaded areas in Figure 6b, top. Consequently, there is a lower peak probability for the accumulated value to lie within the "facilitation region" at any given time. The fact that our data line up nicely when using an exponent of 0.75 for calculating stimulus "energy" suggests in the context of this explanation that the rate of rise of the signal is proportional to contrast$^{0.75}$. If we take this rate to be proportional to the instantaneous neural response, an exponent of 0.75 compares favorably with the compressive contrast responses found in lower visual areas (e.g., Carandini, Heeger, & Movshon, 1997; Sclar, Maunsell, & Lennie, 1990). Clearly, the illustration of a single signal and linear rise to threshold in Figure 6b is a simplification. Nevertheless, the observed invariant "energy" and the increase in curve amplitude with contrast (Figure 6a) are consistent with the view that facilitation and suppression do not depend on two unrelated neural processes but instead on the level of advancement of a progressive neural process. We elaborate on this idea in the Discussion section.

## Discussion

We have shown that prior exposure to a pattern can both facilitate and suppress its initial dominance in binocular rivalry. Facilitation occurs with prior stimuli that are short and/or of low contrast, whereas suppression is observed using high-contrast, long-duration prior stimuli. These effects are in part eye-based and in part pattern-based, they are to a considerable extent retinotopic and show a partial dependence on spatial phase. Our findings stand among a number of examples where processing is inhibited by prior stimuli of long duration, but enhanced by brief ones. An overview of such instances is given by (Huber & O'Reilly, 2003), who focused mainly on higher level cognition, but also within the realm of ambiguous perception there is accumulating evidence that this is a general feature. For instance, in structure-from-motion rivalry prolonged prior exposure to a disparity-disambiguated stimulus impairs initial dominance (Nawrot & Blake, 1989), but brief

exposure has the converse effect (J.B. and T.K., unpublished observations). Such antagonism between long and short prior stimuli has further been found in ambiguous motion perception (Kanai & Verstraten, 2005) and Necker cube rivalry (Long, Toppino, & Mondin, 1992).

In previous cases of combined facilitatory and suppressive effects of prior stimulation, these two effects have commonly been ascribed to two entirely distinct mechanisms. Suppression is often thought to be the result of satiation or "fatigue"-type processes in neurons that code the previewed stimulus (e.g., Huber & O'Reilly, 2003; Long et al., 1992), whereas facilitation has been attributed to a number of other factors, including cognitive expectancy (Long et al., 1992) and integration of the response to the test stimulus with a persisting response to the prior stimulus (Georgeson & Georgeson, 1987; Huber & O'Reilly, 2003; Pinkus & Pantle, 1997). We do not think cognitive expectancy can explain the present data because these bear the stamp of a fairly low-level phenomenon, depending in part on retinal location, eye of origin, and stimulus phase. Similarly, temporal integration of the prime and the test response does not seem adequate because it can only apply to our situation if it takes place at relatively high processing stages, where cells' temporal properties fit the data (Huk & Shadlen, 2005; Keysers & Perrett, 2002). The faster neural responses in lower visual areas (Breitmeyer, 1984) might just be persistent enough to allow facilitation to survive a 165-ms blank interval, but it is unlikely they could explain the buildup of facilitation over up to 500 ms (Figure 2). If not expectancy or neural persistence, what can explain the facilitation we observe? The analysis of Figure 6 indicates that, instead of assuming entirely separate mechanisms for facilitation and suppression, it may be useful to think of both as distinct products of one continuous neural mechanism.

In light of this idea, it is relevant to discuss a recent publication by our laboratory (Noest, Van Ee, Nijs, & Van Wezel, 2007), which addresses the effects of *ambiguous* prior stimuli on initial dominance. An established example of such effects is so-called perceptual stabilization of ambiguous stimuli: The tendency, when an ambiguous stimulus is periodically removed from view, for the same percept to gain dominance on many consecutive reappearances (Leopold et al., 2002; Orbach, Ehrlich, & Heath, 1963; Pearson & Clifford, 2005). Arguably, this stabilization reflects the repeated action of a facilitatory effect of dominance during one (prior) ambiguous presentation on dominance during the following (test) presentation. Noest et al. (2007) systematically varied the timing of such an intermittent presentation cycle and found that in certain temporal regimes, this facilitatory effect changes into an opposite, suppressive effect (as had been suggested by previous findings, Kornmeier & Bach, 2005; Orbach, Zucker, & Olson, 1966). That is, in those timing regimes, subjects tend to see the percept opposite to the previous percept on each presentation. Of note, Noest et al. account for these findings using a model that treats both the facilitatory and suppressive effect as distinct manifestations of one continuous neural process. Specifically, in this model, the rivalrous prior stimulus exerts its effect via progressive sensitivity changes, or adaptation, of neurons coding the dominant percept. In temporal regimes where adaptation is still high at the onset of the new stimulus, the model predicts suppression, whereas in temporal regimes with lower adaptation at stimulus onset it produces facilitation. This mechanism is very similar to the one suggested in Figure 6, where suppression and facilitation are also proposed to depend on the degree of progression of a cumulative process that occurs during the presentation of the prior stimulus. Indeed, in simulations with this model we can reproduce our present data (see Appendix A), when using a nonrivalrous prior stimulus as input instead of the rivalrous input for which the model was designed. This indicates that the effects of unambiguous prior stimuli observed in the present work may reflect similar mechanisms as the effects of ambiguous prior stimuli observed elsewhere. Having said this, it is important to point out several nuances, as not to reduce these ideas to an overly simple "linear rise to threshold" explanation such as used for illustration in Figure 6b. First, in Figure 6b facilitation is simply postulated to change into suppression at some arbitrary threshold level of the accumulating signal. In the model by Noest et al., on the other hand, this transition between both behaviors is much less artificial. There, it is a natural consequence of the assumption that adaptation not only has a conventional divisive effect on activity but also has a slight additive effect. Which of the two opposed forces decides dominance at stimulus onset is determined, in part, by the level of adaptation, leading to the observed transition from facilitation to suppression (Noest et al., 2007). Second, although we believe ambiguous and unambiguous prior stimuli may both engage similar neural mechanisms, there is at least one clear difference. An unambiguous prior stimulus differentially adapts the corresponding neural processing stream from the very lowest level upward (indeed, our data support the view of adaptation on several levels simultaneously; see Figures 3 and 4b). An ambiguous prior stimulus, on the other hand, contains equal evidence for both percepts and therefore arguably adapts both processing streams equally up to some level where the conflict is resolved. Only from this level onward, there is greater adaptation of the dominant representation. As discussed by Noest et al., differential adaptation prior to the stage of conflict resolution (as occurs using unambiguous prior stimuli) can shift the balance between facilitation and suppression at stimulus onset and has a tendency to shift the balance toward suppression. Differences such as these may contribute to known phenomenological differences between the effects of ambiguous and unambiguous prior stimuli. For instance, contrary to the situation with unambiguous prior stimuli, the facilitating effect of ambiguous prior stimuli does not require the prior stimulus to be of low contrast.

Also, the facilitating effect of ambiguous prior stimuli can survive much longer blank intervals than the effects observed in the present work (Leopold et al., 2002).

Our data suggest that the reason that flash facilitation has hitherto been overlooked in experiments, such as the present ones, is that experimenters commonly use relatively long, high-contrast prior stimuli, no blank interval prior to the test, and a black background. All these factors shift the balance between facilitation and suppression toward the latter. In hindsight, influences of the blank interval and background luminance seem reasonable. Without a blank interval, the added stimulus half may benefit from the strong transient response at its onset (Keysers & Perrett, 2002). In fact, a nearby stimulus onset can cause a percept to fade even without interocular conflict (Kanai & Kamitani, 2003; Wilke, Logothetis, & Leopold, 2003). Regarding background luminance, a black background could aid suppression because it increases the strength of the prior stimulus in several ways. First, the observed eye-based effects may be partly luminance based; second, there is a large contrast step between the stimulus and a black background; and third, a black background means a higher *effective* stimulus contrast in case luminance gain control integrates over an area larger than the stimulus itself.

A phenomenon that seems related to flash facilitation is the facilitatory influence of attention on rivalry dominance: Cueing attention to a pattern enhances its probability of gaining initial dominance in subsequent rivalrous viewing (Chong & Blake, 2006; Kamphuisen et al., 2007; Mitchell et al., 2004). It is likely that with flash facilitation, we have at least partly probed the same mechanisms as researchers who studied attention effects. For one thing, the onset of the prior stimulus in our experiments likely draws attention to the previewed pattern (e.g., Corbetta & Shulman, 2002), so in that sense existing attention studies may provide a partial explanation for the present findings. Conversely, we may also consider that the present findings provide a new perspective on existing attention studies. On a neural level, attending to a pattern is in some respects similar to a slight increase in its contrast (e.g., Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000), so our conclusions regarding facilitation may in part also apply to facilitation due to attention. Our results suggest that a kind of gradual contrast-dependent gain control underlies the present observations, raising the possibility that a similar mechanism contributes to the attention effects on initial dominance observed in previous studies. We should note, however, that there is at least one qualitative difference between flash facilitation and attention effects, namely, that the latter seem to lack an eye-based component: When attention is drawn to a monocular stimulus that is then presented to the other eye during the test, it stays associated with the primed pattern (Kamphuisen et al., 2007), with no sign of an opposed eye-based effect (cf. Figure 3c).

We may also consider the possible relation between our findings and those by O'Shea and Crassini (1984). They found that brief intermittent presentations of a binocular rivalry stimulus give rise to apparently normal rivalry alternations, even if the two half-images are presented asynchronously. The effect persists for asynchronies between the two half-images up to about 150 ms, which is similar to the blank durations our facilitatory effect can bridge. One specific observation of O'Shea and Crassini is that the range of effective onset asynchronies is relatively independent of the duration of the individual presentations, suggesting that the onset-to-onset duration (rather that the blank duration) is the relevant variable. To test if something similar applies to our findings, we replotted the data in Figure 2 as a function of the duration between the onset of the prior stimulus and that of the test stimulus (not shown). This, however, yielded rather dissimilar curves for the various blank durations we used, suggesting that the onset-to-onset duration was not a key variable in our experiment. This suggests that the O'Shea and Crassini findings are not directly related to ours.

Prior exposure can also have facilitatory and inhibitory effects in situations that do not involve perceptual ambiguity. A well-known example is masking: Altered detection or judgment of a pattern due to an immediately preceding "mask" stimulus. Like investigators of flash suppression (Kreiman, Fried, & Koch, 2005; Wolfe, 1984), we argue that masking is distinct from the present findings because it shows very different parameter dependencies. Among other features, facilitatory masking effects are restricted to mask–stimulus intervals below about 50 ms (Georgeson & Georgeson, 1987), whereas we find facilitation even at 165 ms blank intervals (Figure 2). There are several other examples where a visual pattern is detected more easily or elicits a faster response, in case it has previously been presented. Like the present effects, those phenomena often have characteristics that indicate the involvement of sensory cortical areas (e.g., Campana, Cowey, & Walsh, 2002; Tanaka & Sagi, 1998), and their temporal properties do not exclude an overlap with the present phenomena either. It seems unlikely that the mechanisms probed in this study are entirely restricted to situations of perceptual ambiguity. We think it would be an interesting subject of future research to search for a direct association between effects of prior stimuli on initial dominance on the one hand, and on detection or reaction times on the other.

# Appendix A

## Individual subjects

Figure A1 shows the individual subjects' data that underlie the top panel of Figure 2. All subjects show the

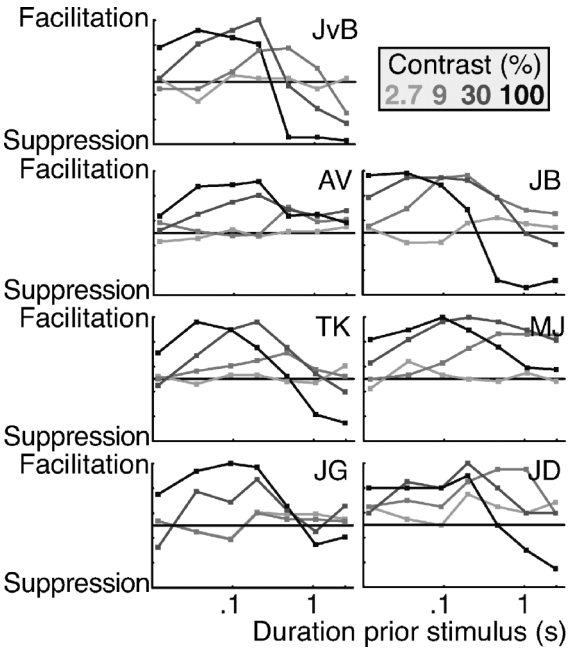


Figure A1. Individual subjects' data from our main condition, at a 71-ms blank duration. All subjects show the same trends.

same trends, although there are clear differences both in the temporal evolution of the patterns and in the relative importance of facilitation versus suppression.

## The effect of a prior stimulus on orientation discrimination

Because our main measure consisted of observers' subjective perceptual judgment, we wished to make sure that our findings were not due to a cognitive bias. The results from Figures 2 and 3 were obtained within the same sessions by randomly interleaving conditions, and the fact that these figures show very different outcomes for subjectively identical prior stimuli (depending on eye of origin) took away much of our concern. Nevertheless, two authors performed an additional control experiment where we quantified the effect of a prior stimulus objectively, as change in orientation discrimination performance. We used the experimental sequence of our main condition but with the instruction to report whether the right-tilted test grating was rotated clockwise or counterclockwise from 45°. In agreement with our previous results, for brief prior stimuli, performance was best when the prior stimulus was the right-tilted grating (flash facilitation, left column in Figure A2), and for long prior stimuli, performance was best when it was the opposite grating (flash suppression, right column in Figure A2). The effect of prior stimulation does therefore not depend on a subjective dominance judgment.

## A model for the effects of rivalrous and nonrivalrous prior stimuli

Like many rivalry models (Wilson, 2005), the model by Noest et al. (2007) comprises, for each of the competing neural representations, two differential equations: one for the representation's activity and one for its adaptation, respectively,

$$\tau \partial_t H_i = X_i - (1 + A_i)H_i + \beta A_i - \gamma S[H_j] \quad \text{(A1)}$$

and

$$\partial_t A_i = -A_i + \alpha S[H_i]. \quad \text{(A2)}$$

Here $\tau \ll 1$ is a time constant, $H$ is the activity, $X$ is the input strength, and $A$ is the adaptation. $\gamma$ and $\alpha$ are constants governing the strengths of cross inhibition between the representations and the adaptation, respectively. A notable difference between this model and other ones is the term $\beta A$, which describes an additive effect of adaptation on activity. It is this term that allows adaptation $A$ to facilitate dominance in some conditions.

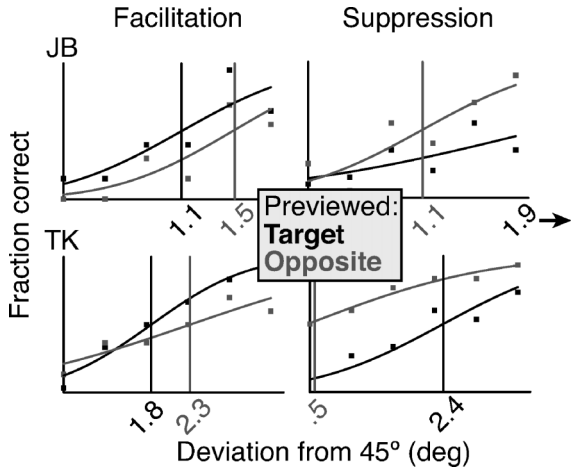


Figure A2. Orientation discrimination performance as a measure of facilitation and suppression. In case of a weak prior stimulus (100% contrast, 94 ms), performance was better if the prior stimulus was identical to the grating on which an orientation judgment was required. With a strong prior stimulus (100% contrast, 2.5 s), this pattern reversed. This indicates that flash suppression and flash facilitation are not due to a cognitive bias in subjects' subjective dominance reports. Vertical lines mark the means of the cumulative Gaussians fitted to the data. We determined subjects' baseline thresholds beforehand in a staircase procedure and made sure we used prior stimuli that in the main condition yielded robust facilitation and suppression, respectively. All points represent 40 measurements. The effects of facilitation and suppression are significant both within subjects (bootstrap, $p < .05$) and combined over both (one-sided paired $t$ test, $p < .05$).

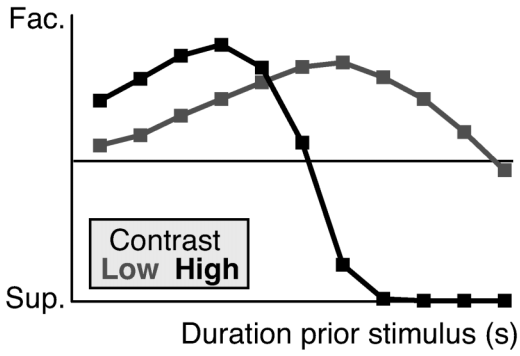


Figure A3. Simulation results using the model by Noest et al. (2007). Although developed to describe the effect of a rivalrous prior stimulus on initial dominance, the model qualitatively accounts for our data as well.

Subscripts $i$ and $j$ refer to the two percepts, and $S[X]$ is a sigmoidal function of $X$, here we used

$$S[X] = \frac{X^2}{1 + X^2}, \quad \text{(A3)}$$

for $X > 0$, and $S[X] = 0$ otherwise. Simulations were performed at the following parameter settings. During the test phase, $X_i = X_j = 0.6$ and during the blank $X_i = X_j = 0$. For the prior stimulus, $X_i = 0$ and $X_j = 0.4$ or $1.0$ to simulate a low or high contrast, respectively. The constants were set to $\tau = 0.02$, $\gamma = 3.3$, $\alpha = 4$, and $\beta = 0.2$. The duration of the prior stimulus was varied from $10^{0.1}$ to $10^{2.1}$, and the blank interval was 8. The one modification we made to the original model is that we included a noise term in the adaptation equation, namely, additive Gaussian noise of $\mu = 0$ and $\sigma = 2.5$, at an integration step size of 0.1. Figure A3 shows that at these settings the model qualitatively reproduces our main result.

As a final remark, note that we focus on the general principle that the mechanism employed by this model can explain our data. A quantitative application of the model to our data is complicated by the fact that here adaptation occurs, not only at the level where rivalry is resolved ($A$), but also at all levels leading up to it, causing an asymmetry in the input strengths $X$ (Noest et al., 2007, Figure A2; see also Discussion section). Adding these stages to the model would allow for too much freedom (for instance, adaptation time constants and contrast gain functions could be chosen for each stage independently), leaving it underconstrained by our data.

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